
TAXONOMIC REVISION OF *CRUCKSHANKSIA* AND *OREOPOLUS* (RUBIACEAE: HEDYOTIDEAE)¹

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ABSTRACT

Oreopolus is here distinguished based on its ternate leaves, triangular entire to shortly mucronate or bilobed stipules, simple inflorescence bracts that resemble stipules, and calyx lobes that do not enlarge in fruit; thus circumscribed it includes only *O. glacialis* (Poepp.) Ricardi. *Cruckshanksia* is distinguished by opposite to subalternate leaves, erose bilobed stipules, 2–7-lobed inflorescence bracts that resemble the leaves, and calyx lobes that are markedly enlarged in fruit; seven species are recognized here. Keys and complete descriptions, nomenclature, and distributional information are presented.

The taxonomy and study of *Oreopolus* Schlttdl. and *Cruckshanksia* Hook. & Arn. (Hedyotideae; Puff, 1988; Robbrecht, 1988) have been closely intertwined since these genera were first described. The type species of *Oreopolus* was first described in *Cruckshanksia*, and two other species, *C. macrantha* Phil. and *C. palmae* Clos, have been alternatively treated in *Oreopolus* by some authors (e.g., Ricardi, 1963a). Both of these genera are endemic to temperate South America and share generally similar habits, corollas, and fruit, including several unusual features, and they appear to be closely related. These plants are characteristic of cool dry sites from near sea level to as high as 3500 m in the northern end of their range. *Cruckshanksia* is found at low to high elevations in arid central to northern Chile, with two species, *C. macrantha* and *C. hymenodon* Hook. & Arn., extending into adjacent Argentina. *Oreopolus glacialis* (Poepp.) Ricardi is found in the Andean Cordillera from central Chile and Argentina south into Tierra del Fuego.

These two genera share papery to membranaceous capsules with loculicidal dehiscence and two ovules per locule, with the ovules borne on an elongated pseudoseptum (Fig. 1A, B). This pseudoseptum is attached peltately to the true septum and extends at right angles from it into the locule. The genera also resemble each other in their low, usually geophytic or cryptophytic habit and distylous flowers with bright yellow salverform corollas with

slender tubes. However, *Oreopolus* can be separated by its usually ternate leaf arrangement, entire triangular stipules that are usually imbricate by the poor development of internodes, floral bracts that resemble the stipules, and calyx lobes that do not enlarge markedly in fruit. In contrast, opposite to occasionally subalternate leaf arrangement, erose usually deeply bilobed stipules separated by well-developed internodes, inflorescence bracts that resemble the cauline leaves, and calyx lobes typically enlarging markedly in fruit distinguish *Cruckshanksia*. Additionally, *Cruckshanksia* is distinguished by its inflorescence bracts and in some species cauline leaves that are deeply 2–6-lobed, an unusual feature. Several species are also notable for the prolongation of one or more of the calyx lobes into a stipitate petaloid appendage.

All of the species treated here were first described in *Cruckshanksia*, and were retained in that genus until recently (e.g., Schumann, 1891; Muñoz, 1966). This group was studied in detail by Ricardi (1963a, b, 1968, 1973; Ricardi & Quezada, 1963), who first separated *Oreopolus* with only one species (Ricardi, 1963a). Later Ricardi (1973) restricted *Cruckshanksia* to seven species with well developed petaloid calyx lobe appendages and transferred two species that lack these structures to *Oreopolus*.

GENERIC LIMITS

Regardless of how they are delimited from each other, *Cruckshanksia* and *Oreopolus* share a dis-

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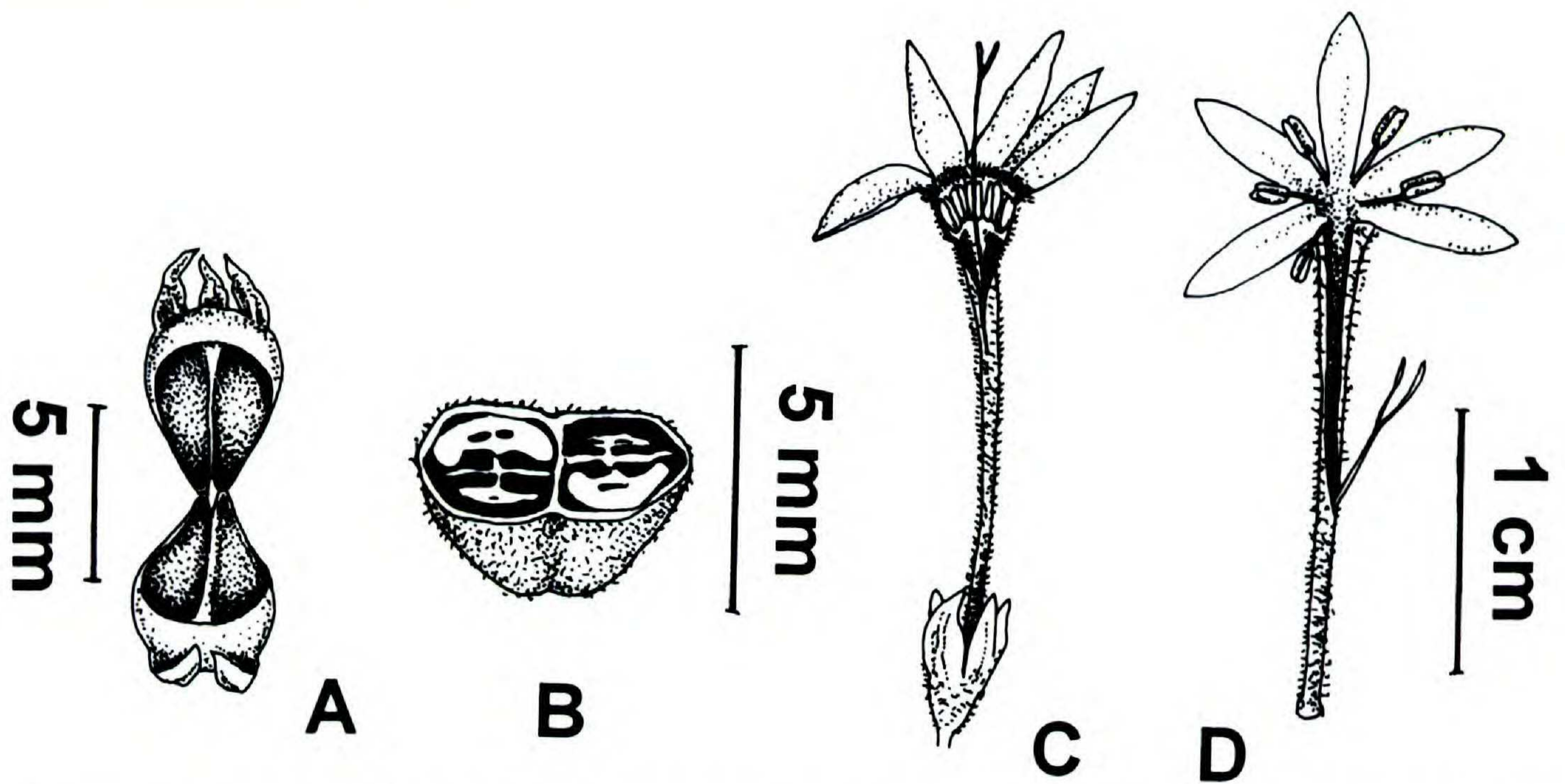


Figure 1. Fruit and floral details of *Oreopolus glacialis*.—A. Dehiscent capsule that contained two developed seeds.—B. Cross section of capsule containing two developed seeds.—C. Long-styled flower, partially dissected.—D. Short-styled flower, partially dissected. A, B from Ricardi (1963a: fig. 3C, F); C, D from Ricardi (1963a: fig. 2B, D). C, D to same scale.

tinctive and apparently unique ovary arrangement, as well as distylous flowers with similarly shaped salverform yellow corollas. Based on the ovary arrangement, these genera appear to be closely related.

As circumscribed by Ricardi (1963a), *Oreopolus* included three species and was distinguished by its capsules dehiscent into two valves and flowers lacking petaloid calyx lobe appendages, while *Cruckshanksia* included seven species (two of which are not recognized in the current treatment) and was distinguished by its capsules dehiscent into four valves and flowers each with one or more petaloid calyx lobe appendages (Ricardi & Quezada, 1963; Ricardi, 1963a). However, two species that Ricardi placed in *Oreopolus*, “*O. macranthus*” (*C. macrantha*) and “*O. palmae*” (*C. palmae*), were not known in fruit according to his own descriptions (Ricardi, 1963a), and another species that he placed in *Cruckshanksia*, *C. lithiophila*, is so similar to *C. macrantha* that these can be separated only by the size and shape of the mature calyx lobes. Mature capsules of *C. macrantha* and *C. palmae* are now known. In both species the capsules are dehiscent into four or five valves, which either necessitates the transfer of these two species to *Cruckshanksia* and the separation of the genera only by the number of capsule valves, or, if these species are retained in *Oreopolus*, the separation of the genera only by the presence versus absence of petaloid calyx lobe appendages.

Neither of these alternatives takes into consideration several other unusual features, in particular the ternate leaves and membranaceous stipules of *Oreopolus glacialis* and the 3–7-lobed foliaceous inflorescence bracts found in the remaining species. Although Ricardi’s illustration of “*O. macranthus*” (1963a: fig. 5) clearly shows its three-lobed foliaceous inflorescence bracts, this feature was not included in his descriptions of either this species or “*O. palmae*,” although it is present in both taxa, nor was it mentioned in the genus description he presented for *Oreopolus*. All of the species studied here except *O. glacialis* also share well-developed calyx lobes that persist and usually enlarge markedly on the fruits, and filamentous erose appendages on the calyx limb and also on at least some of the stipules and inflorescence bracts. These unusual features support the circumscription of an apparently monophyletic group comprised of all the species studied except *O. glacialis*. Therefore, *Oreopolus* is here circumscribed to include one species, *O. glacialis*, while the other two species included in this genus by Ricardi are here assigned to *Cruckshanksia*.

The two species here transferred back to *Cruckshanksia*, *C. macrantha* and *C. palmae*, do not bear petaloid calyx lobe appendages but do share with the other *Cruckshanksia* species relatively large calyx lobes that are narrower at the base than at the middle and are enlarged in fruit, in contrast to the smaller triangular lobes of *Oreopolus*, which are

broadest at the base and do not enlarge at all in fruit. This revised classification also eliminates the problem of placing two very similar species, *C. macrantha* and *C. lithiophila*, in separate genera, even though these are so similar that when they are in flower they cannot always be separated with confidence.

The characters that are used here to distinguish *Oreopolus* from *Cruckshanksia* are summarized in the key to the genera presented in the taxonomic treatment, below. In the following morphological survey, *Oreopolus* and *Cruckshanksia* are compared as they are delimited in the taxonomic treatment.

MORPHOLOGY OF *OREOPOLUS*

Habit. Plants of *Oreopolus* are perennial hemi-cryptophytes originating from woody taproots. They form dense low cushions to 75 cm in diameter in open sand or exposed hard soils or rubble.

Stems. The stems are stout and the internodes are usually very shortly elongated at most, usually to less than the length of the stipules, so that these overlap.

Vesture and crystals. The vegetative portions of the plants range from completely glabrous to moderately or sometimes densely puberulous with short unicellular or uniseriate trichomes. The plants contain raphides, although these may be difficult to observe in succulent tissues.

Leaves. The leaves are ternate or rarely opposite, shortly petiolate, simple, and lack domatia. The venation is generally pinnate, although often only the midrib is visible. The cauline leaves are all similar.

The stipules are interpetiolar and fused to the bases of the petioles (Fig. 2A). They are generally triangular in shape, though frequently shortly mucronate or sometimes shortly bilobed at the apex, with entire margins. They are membranaceous and usually nearly hyaline.

Inflorescences. The flowers are terminal and solitary, or terminal and axillary and borne in congested groups of two to six. Each flower is subtended by bracts that resemble reduced stipules, and are triangular, membranaceous, and entire along the margins, but are acute rather than bilobed at the apex. The leaves at the distalmost nodes exceed and usually to some extent enclose the inflorescences.

Flowers. The flowers are hermaphroditic and distylous (Fig. 1C, D). Long-styled and short-styled forms are represented on herbarium specimens in approximately equal proportions, and frequently are found mixed in the same collection when more

than one plant was sampled. These forms differ in relative style lengths, point of insertion of the stamens, degree of development of the filaments, and form and pubescence of the corollas. The stigmas are exerted in all mature long-styled flowers seen (in contrast to the apparently delayed elongation of the style in *Cruckshanksia*; see below).

The ovary is inferior and bilocular, turbinate in shape, and pilosulous. Ovary pubescence is not correlated with pubescence of the vegetative parts. Each locule contains two ovules, which are attached to elongated axile placentas that extend perpendicularly from the septum into the locules to form pseudosepta that almost completely subdivide each locule (Fig. 1B). The ovules are anatropous.

The calyx limb may be glabrous or puberulous, and is deeply five-lobed with the lobes generally similar in size and shape. The lobes are triangular to lanceolate, with an acute or sometimes shortly emarginate apex. Colleters have not been seen.

The corollas are salverform with slender cylindrical tubes and five triangular lobes with valvate aestivation. They are pale to usually very bright yellow throughout. The shape of the tube is dimorphic, with the tubes of the short-styled form uniformly cylindrical in contrast to those of the long-styled form, which are swollen for several millimeters at the top to accommodate the included anthers (Fig. 1C, D). This swollen portion of the long-styled form was referred to as the "garganta" by Ricardi and Quezada (1963). The pattern of pubescence is also dimorphic: both the long-styled and short-styled forms are similarly puberulous to pilosulous externally (abaxially) in the tubes and on the lobes, but the short-styled form is glabrous internally (adaxially) throughout the tube while the long-styled form is glabrous in the lower portions of the tube but barbate in the throat.

The five stamens are inserted at the top of the corolla tube in short-styled flowers, and at the base of the throat swelling in long-styled flowers. The anthers of short-styled flowers are exerted on slender, usually flattened filaments, while those of long-styled flowers are subsessile and included. The anthers of both floral forms are narrowly oblong and dehiscent by longitudinal slits.

The style is slender and filiform, in the short-styled form extending to only a little beyond the middle of the corolla tube and in the long-styled form shortly exceeding the corolla tube. The paired stigmas are linear and papillose on the adaxial surface but glabrous on the abaxial surface in both floral forms. The disk is not evident ("not developed," Ricardi & Quezada, 1963, my translation from the Spanish).

Infructescences and fruit. The infructescences do not differ in form from the inflorescences. The fruit is a papery- to chartaceous-walled obovoid capsule that is somewhat flattened laterally. The capsule is dehiscent loculicidally and apparently basipetally into two valves. The calyx limb is persistent on the capsule, frequently becoming split completely between the lobes.

The seeds are planoconvex to somewhat obovoid and somewhat flattened, with a smooth brown to black seed coat. A median sulcus on one side marks the site of attachment to the placenta, and at dispersal some placental material frequently remains attached here. The seeds of *Oreopolus* are similar to those from species of Rubiaceae with only one ovule and seed per locule and two per fruit; however, because the placenta is enlarged perpendicularly to the septum in *Oreopolus* the seeds are borne at right angles to the true septum, so the sulcus is on the lateral face and the true adaxial face is smooth.

MORPHOLOGY OF *CRUCKSHANKSIA*

Habit. Plants of *Cruckshanksia* are perennial or sometimes annual geophytes or hemicryptophytes originating from ropelike woody taproots and underground stems with corky, usually red-brown bark, except for those of *C. pumila*, which are typically annuals with a smooth gray to brown epidermis. The perennial plants generally form loose circular clumps to as much as 40 cm in diameter, with the above-ground stems weak to reclining. Most or all stems die back to the ground during dry or cold periods. The annual plants of *C. pumila* may grow to 15 cm tall and branch several times, but may also flower at only 3–4 cm tall, with the flowers produced from the second stem node above the cotyledons. Individual plant size in this species may be correlated with microsite water supply.

Stems. The taproots of the perennial species usually produce four to ten or more separate slender stems. These may be borne above or below ground. Some species, notably *Cruckshanksia macrantha* and *C. lithiophila*, typically have twenty to thirty or more of these stems. Axillary buds are often well developed and frequently densely pubescent.

The above-ground stems are generally slender, with well-expanded internodes. More basal internodes are generally quadrate while those at more distal nodes are subterete to irregularly angled or channeled. Although Ricardi and Quezada (1963) used the relative lengths of the more proximal internodes to distinguish species, this character ap-

pears to vary with local environmental conditions and is not considered taxonomically reliable here.

Vesture and crystals. Plants of *Cruckshanksia* are generally puberulent to densely villosulous or shortly pilosulous, with short unicellular or uniseriate trichomes found on most or all parts of the plant distal to the hypocotyl. The plants contain raphides.

Leaves. The cauline leaves are opposite or occasionally subopposite to alternate at more distal nodes, and lack domatia. The venation is generally subpalmate, with one to two pairs of strongly ascending secondary veins arising in the basal third or half of the blade. In species with very narrow leaf blades (*Cruckshanksia verticillata*, *C. montiana*), only the midrib may be evident and sometimes even this cannot be distinguished. In annual plants of *C. pumila*, the cotyledons are usually persistent on the flowering and sometimes also the fruiting plants.

The cauline leaves at the more basal nodes are simple or they may be deeply two- to three-lobed in some individuals of *Cruckshanksia verticillata*. The leaves of more distal nodes may be consistently simple and distinct from the lobed “floral leaves” or foliaceous inflorescence bracts (“hojas florales” and “pseudotrifolios” sensu Ricardi and Quezada, 1963) in *C. palmae*, *C. macrantha*, and *C. lithiophila*, or in the remaining species the cauline leaves at the upper stem nodes may vary from simple to lobed and intergrade with the floral bracts. Simple leaves taper to an acute, usually short-petiolate base; the lobed leaves are cuneate to rounded at base and sessile to subsessile. The lobed cauline leaves of several species (notably *C. montiana* and *C. hymenodon*) often bear linear multicellular appendages on the margins near the bases of the lobes, and sometimes in the sinuses between the lobes. These structures were apparently referred to as “escamas” by Ricardi and Quezada (1963), and are perhaps comparable to the erose marginal projections found on the stipules (see below).

Stipule morphology typically varies on an individual plant. At more basal nodes bearing simple leaves and at the cotyledon-bearing nodes of annual plants, the stipules are interpetiolar and may be free or fused to the petioles (Fig. 2B). The interpetiolar portion may be triangular or shortly bilobed, and entire or somewhat erose. At progressively more distal nodes, the stipules typically are progressively more deeply bilobed and more erose, with the linear marginal appendages up to several millimeters long (Figs. 2C, E). At stem nodes closest to the inflorescence, the stipules are sometimes completely divided into two lobes, which may be

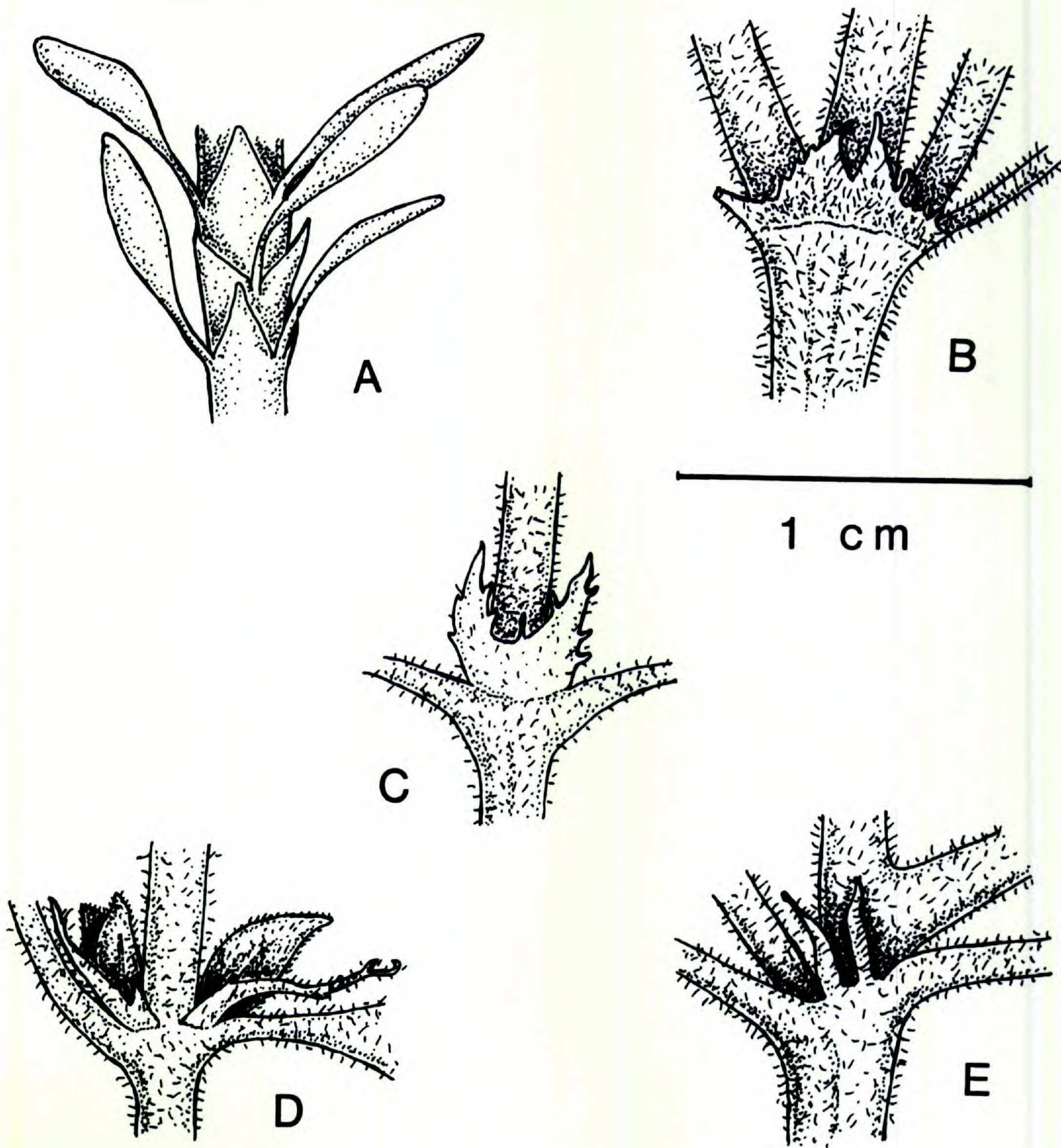


Figure 2. Stipule morphology of *Oreopolus* and species of *Cruckshanksia*. —A. *O. glacialis*, node near middle of stem. —B. *C. hymenodon*, node near base of stem. —C. *C. montiana*, node near middle of stem. —D. *C. hymenodon*, node immediately below inflorescence. —E. *C. hymenodon*, node near middle of stem. All to same scale. A based on Donat 172, MO; B, E based on Taylor 10782, MO; C based on Gay s.n., MO-393317; D based on Taylor 10781, MO.

connected by an interpetiolar line or may show no connection at all (Fig. 2D). These lobes are frequently fused to the petioles, and typically have strongly erose margins. In several species (notably *Cruckshanksia hymenodon* and *C. pumila*), the stipules of distal stem nodes are often irregular: only one lobe on one side may be developed, or one lobe may be well developed and free while the other lobe is reduced and fused to the leaf. Irregularly lobed cauline leaves are subtended by irregular stipules, and three-lobed cauline leaves lack stip-

ule lobes. Ricardi and Quezada (1963) used degree of stipule lobing to distinguish species, but this feature seems to vary with developmental stage on an individual plant, and several degrees of lobing are typically found on a single stem. This feature is not considered taxonomically reliable here.

The correlation between irregular stipule development and lobed leaf shape suggests that the lobed leaves could be formed by a fusion of expanded stipule lobes and the leaf blade, as in *Galium* L. and some *Knoxieae* (Robbrecht, 1988). In

this case the lateral leaf lobes would be equivalent to expanded stipule lobes. This possibility is supported by the lack of stipule lobes subtending these leaves, and their sessile rather than petiolate bases. The linear appendages on lobed leaves would then be equivalent to the erose projections characteristic of the stipule margins. More detailed study is needed to evaluate this possibility.

Inflorescences. The inflorescences are terminal, dichasial to somewhat irregular, strongly congested to subcapitate cymes. The flowers are sessile to subsessile (Fig. 3A). Ricardi and Quezada (1963) reported that the flowers of *Cruckshanksia montiana* are borne on pedicels to 2 mm long, but the structures they measured are similar to those they called inflorescence branches in other species, and are considered inflorescence branches here.

Each flower is subtended by an unlobed or usually three- to seven-lobed "floral leaf" or foliaceous inflorescence bract that encloses the flower bud until anthesis (Fig. 3A, B). These structures have been variously referred to as leaves or bracts by different authors; they are here considered bracts based on their position, subtending the individual flowers of a cymose inflorescence, and usually different form from the cauline leaves. This interpretation agrees with that of Jansen (1979) for *Kajewskiella* Merr. & Perry, in which inflorescence bracts are frequently subopposite or alternate and bear colleters. Jansen considered these bracts to be homologous to leaves, although with the problem that colleters, which are typically found on inflorescence bracts of *Kajewskiella*, are normally found on stipules but not leaf blades or petioles. The presence of colleters in the inflorescence bracts of *Cruckshanksia* suggests that not only are the bracts generally homologous to leaves, but that they are homologous to the entire leaf, including the stipules, as proposed also for *Gaertnera* Lam. (van Beusekom, 1967).

The inflorescence bracts of *Cruckshanksia* are generally similar in color, size, and pubescence to cauline leaves, and in those species that occasionally have lobed cauline leaves (notably *C. hymenodon* and *C. pumila*), leaves and bracts may intergrade (see above).

Flowers. The flowers are hermaphroditic, and are distylous in all species of *Cruckshanksia*. (Although Ricardi & Quezada (1963) reported that several species had only one floral form, both have now been found for all species.) Long-styled and short-styled forms are represented in living populations of *C. pumila* and *C. hymenodon* (pers. obs.) and in herbarium specimens of all species in approximately equal numbers. The forms differ in rel-

ative style length, point of insertion of the filaments, and form of the corolla. In long-styled flowers the style apparently elongates after anthesis; this one floral form may have a stylar or "ixoroid" pollen presentation mechanism (Robbrecht, 1988), which implies that these flowers are also protandrous. The presence of this mechanism has not previously been seen in distylous flowers and must be confirmed by field study, but such a mechanism is suggested by the pilosulous pubescence on the uppermost portion of the style and abaxial stigma lobes, to which pollen grains are found adhering in most herbarium specimens that have the style elongated and the stigmas exerted.

The ovary is inferior and bilocular, turbinate or somewhat ovoid or obovoid, and usually relatively densely pubescent. The ovary and ovules are similar to those of *Oreopolus* (see above).

The calyx limb is pubescent similarly to the vegetative portions of the plant, and deeply to nearly completely divided with a tube portion 1.5 mm long or shorter. Calycine colleters have not been seen. In some species (*C. palmae*, *C. macrantha*, *C. lithiophila*), the calyx lobes are consistently five, equal or nearly so, and elliptic to oblanceolate (*C. palmae*, *C. macrantha*) or slightly to strongly stipitate with the upper portion expanded into a narrowly elliptic to ovate appendage (*C. lithiophila*). In the remaining species the calyx lobes vary from two to five per flower on a single plant, and are usually strongly unequal (Fig. 3A). In these species each flower bears one to four stipitate, appendaged, bright yellow or pink petaloid calyx lobes along with usually one or more shorter triangular lobes, and sometimes also one or more elliptic to oblanceolate lobes similar to the lobes of the inflorescence bracts (these last structures were not described by Ricardi & Quezada, 1963). These petaloid calyx lobe appendages were variously referred to as "sépalos petaloides" and "uñas" by Ricardi and Quezada (1963). The calyx typically also bears erose or linear appendages in the sinuses between the lobes (referred to as "escamas calicinales" by Ricardi & Quezada). These are similar to the erose appendages found on the bracts and stipules.

Strongly and irregularly unequal calyx lobes are found in several genera of Rubiaceae (e.g., *Rondeletia* L., *Pentas* Benth.), and stipitate calyx lobe appendages are also known from other genera of this family (e.g., *Mussaenda* L., *Warszewiczia* Klotsch, *Pogonopus* Klotsch). Such appendages are often brightly colored and are thought to function in attracting pollinators, in which case they are considered semaphylls (Robbrecht, 1988). The ap-

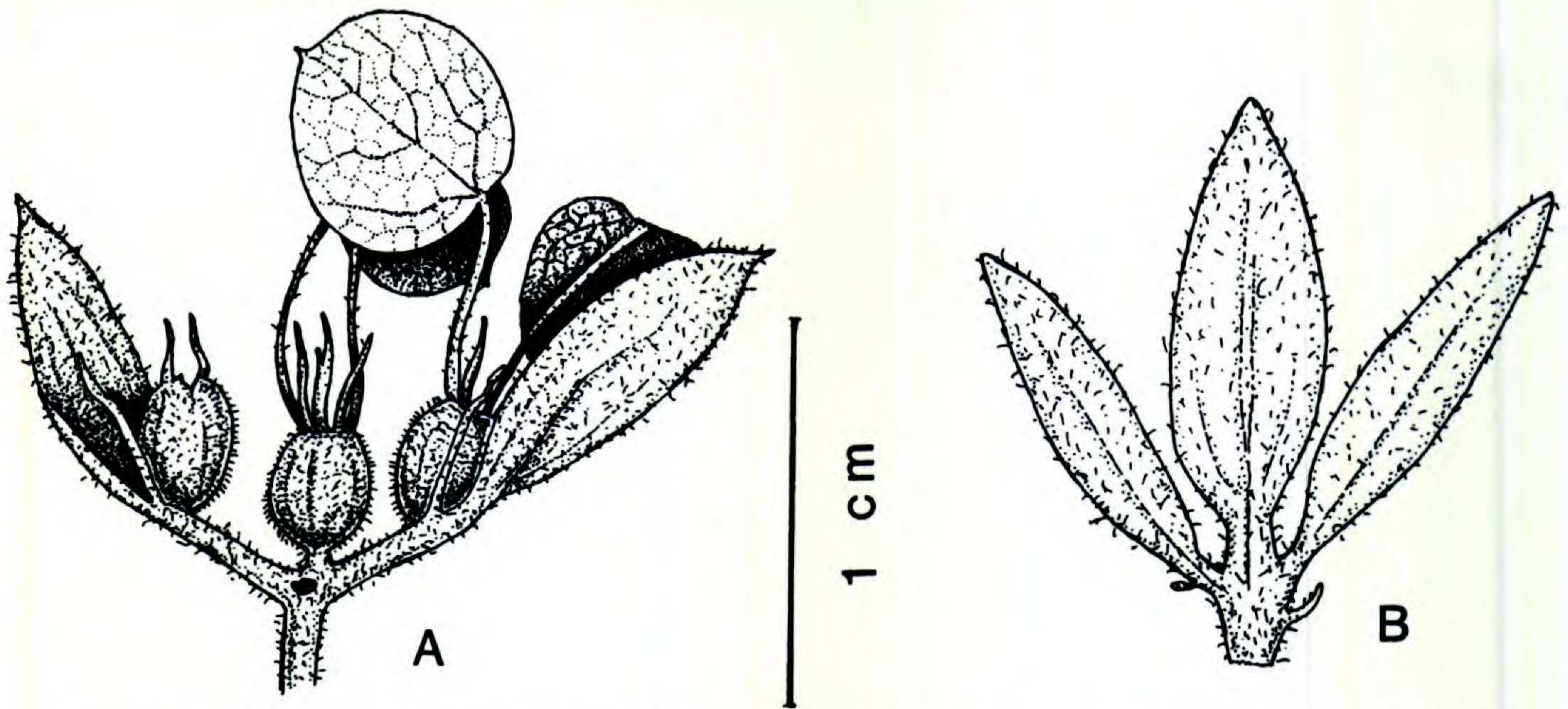


Figure 3. Inflorescence details of *Cruckshanksia hymenodon*.—A. Cymule with immature capsules.—B. Floral bract. Both to same scale. A based on *Mahu s.n.*, MO-3272960; B based on *Wagenknecht 18484*, MO.

pendages found in *Cruckshanksia* are membranaceous, reticulately veined, and generally yellow, or pink to occasionally white in *C. hymenodon*. The form of the appendages changes markedly during development of the flower. In bud they are narrowly elliptic and acutely to obtusely angled at both apex and base. At anthesis in most species they are ovate or elliptic-oblong and rounded to truncate at the base and apex or with a triangular projection and short mucro at the apex. In some species the calyx lobe appendages continue to enlarge markedly as the fruit develops (see below). Previously published descriptions of most *Cruckshanksia* species include measurements of fruiting rather than flowering calyx lobe appendages, probably because the plants usually flower and fruit concurrently and the appendages are larger and more striking in fruit.

Ricardi and Quezada (1963) used the shape of the petaloid calyx lobe appendages to distinguish species. However, this feature is variable, and at best seems to distinguish only developmental stages of an individual flower. Material cited by them frequently shows both of the conditions they used to separate a pair of species on different flowers of the same plant, and this feature is not considered taxonomically reliable here.

The corollas of *Cruckshanksia* are similar in form to those of *Oreopolus* (see above). They are bright to deep yellow and frequently marked with darker yellow on the lobes. The corollas of both floral forms are glabrous internally and on the adaxial surfaces of the lobes, and typically pubescent throughout the external (abaxial) surface. Herbarium specimens of some species, notably *Cruckshanksia hymenodon*, show marked variation in co-

rolla length; this may be real morphological variation, perhaps due to water availability, or it may include differential shrinkage during preparation of dried specimens.

The stamens, style, and stigma are similar to those of *Oreopolus* (see above).

Infructescences and fruit. The infructescences are similar to or often somewhat more expanded than the inflorescences, with the cyme branches elongating to separate the developing fruits (Fig. 3A). The fruit is a papery- to chartaceous-walled, subglobose to ovoid or oblong capsule. The capsule is dehiscent loculicidally, acropetally, and frequently irregularly into two to five valves. In species with variously two to four appendaged calyx lobes, the number of capsule valves often equals the number of appendaged calyx lobes. The illustration presented by Schumann (1891) suggests that the dehiscence is basipetal, but this probably was drawn from a specimen and based on a capsule that was crushed during the drying process; similar capsules can be found on specimens that also have capsules dehiscing from the base. The placentas appear to become fleshy as the capsule matures, and may sometimes be dispersed with seeds still attached.

The calyx limb is persistent on the capsule, and the calyx lobes typically enlarge and sometimes also change shape as the fruit matures. In species in which the calyx lobes are all similar, the lobes typically retain their general shape but become enlarged and papery, and sometimes more strongly narrowed at the base. In species in which the calyx lobes are unequal, the smaller lobes do not change noticeably but the appendaged lobes may enlarge and change form markedly, typically becoming sub-

orbicular to reniform, cordate at the base, and emarginate at the apex, with the triangular apex and mucro becoming inrolled or reduced. At maturity, these appendages are dry, papery, and usually brown, and may function in dispersal or at least dehiscence of the fruit; such structures are considered pterophylls (Robbrecht, 1988).

The seeds are similar to those of *Oreopolus* (see above), except the seed coat may be smooth to rugose.

TAXONOMIC TREATMENT

This work is based on study of herbarium specimens from A, BAB, CONC, CORD, CTES, E, F, GH, K, LP, M, MO, NY, SGO, SI, and UC, and field observations in northern Chile in 1991 and 1993. Measurements given in brackets are taken from Ricardi (1963a, 1963b) and Ricardi and Quezada (1963) but were not observed on specimens studied.

KEY TO THE GENERA

- 1a. Leaves ternate or rarely opposite, thickly succulent drying coriaceous; stipules triangular, entire to shortly mucronate or bilobed, closely set or usually imbricated by the limited development of the internodes; leaves drying coriaceous, ternate or rarely opposite; flowers subtended by triangular membranaceous bracts smaller than but similar to the stipules; calyx lobes 5, triangular, never prolonged into petaloid appendages, not enlarging in fruit; corolla pubescence dimorphic, differing in long-styled and short-styled forms; capsules basipetally dehiscent into 2 valves

..... *Oreopolus*

- 1b. Leaves opposite or sometimes subopposite to alternate at more distal nodes; stipules triangular or shallowly to completely bilobed, entire to strongly erose, separated by elongated internodes; leaves drying chartaceous to subcoriaceous, opposite or sometimes subopposite to alternate at more distal nodes; flowers subtended by simple to usually 3–7-lobed foliaceous bracts similar to the cauline leaves; calyx lobes 2–5(6), elliptic to obovate, subulate, or sometimes prolonged into stipitate petaloid appendages, usually enlarging in fruit; corolla pubescence similar in long-styled and short-styled forms; capsules acropetally dehiscent into 2–5 valves

..... *Cruckshanksia*

Oreopolus Schltld., *Linnaea* 28: 493. 1857.
TYPE: *Oreopolus citrinus* Schltld. [= *Oreopolus glacialis* (Poepp.) Ricardi].

Perennial, rather succulent, hemicryptophytic low shrubs from a woody taproot, glabrous to pubescent, with raphides; stems quadrate to terete, internodes usually not or only shortly expanded. *Leaves* ternate or rarely opposite, simple, shortly

petiolate; *blades* elliptic to lanceolate, thickly succulent, drying coriaceous, without domatia; venation pinnate but usually not evident; *stipules* interpetiolar, fused to petioles, imbricated by poor development of the internodes, membranaceous, triangular, entire to shortly mucronate or bilobed. *Inflorescences* terminal, capitate, sessile; *flowers* 2–6, distylous, each subtended by a bract resembling a reduced stipule, this sometimes deeply divided with age; *hypanthium* turbinate; *ovary* inferior, bilocular, ovules 2 per locule, anatropous, borne on placentas attached to septum and prolonged into a partial pseudoseptum; *calyx* limb deeply 5-lobed, lobes equal, generally triangular; *corolla* slenderly salverform, yellow, in short-styled form the tube glabrous internally and uniformly cylindrical, in long-styled form the tube swollen and barbate at top, lobes 5, triangular to lanceolate, acute, valvate; *stamens* 5, in short-styled form inserted at top of corolla tube, exerted, with flattened filaments, in long-styled form inserted at base of enlarged throat of corolla tube, included, subsessile, anthers in both forms basifixed, narrowly ellipsoid to oblong, dehiscent by longitudinal slits; *styles* filiform; *stigmas* 2, linear, papillose, in short-styled form borne near middle of corolla tube and abaxially glabrous, in long-styled form exerted by several mm and abaxially pilosulous; disk rudimentary. *Fruits* capsular, obovoid, laterally somewhat flattened, papyraceous to chartaceous, dehiscent loculicidally and basipetally into 2 valves, calyx limb persistent, similar to that of flowers; *seeds* planoconvex to obovoid, somewhat compressed, sulcate at attachment, brown, smooth to somewhat rugose.

One species of dry cool regions in the Andean Cordillera, central Chile and Argentina to Tierra del Fuego.

Oreopolus glacialis (Poepp.) Ricardi, *Gayana* 6: 7. 1963. *Cruckshanksia glacialis* Poepp., in Poepp. & Endl., *Nov. Gen. Sp.* 3: 31. 1841. TYPE: Chile. IX Region.³ Prov. Malleco: Volcán Antuco, 8500 ft. [2750 m], Mar. 1829, *Poeppig* 59 (holotype, B not seen, destroyed; isotype, CONC-28779).

Oreopolus citrinus Schltld., *Linnaea* 28: 492. 1857. TYPE: Chile. X Region. Prov. Valdivia: "Cordillera de Rancho, in tierra Pehuelchorum," Dec. 1854, *Lech-*

³ For map of regions in Chile see *Flora de Chile*, Vol. 1, edited by Clodomiro Marticorena and Roberto Rodríguez, published in 1995 by Universidad de Concepción, Chile.

ler/Hohenacker 2895 (holotype, HAL not seen; isotypes, CONC, K, NY, photo (neg. #2479) SGO).

Oreopolus patagonicus Speg., Rev. Fac. Agron. Veterin. La Plata 3(30–31): 525. 1897. *Cruckshanksia patagonica* (Speg.) Macloskie, Rep. Princeton Univ. Exp. Patagonia 8(5): 740. 1905. TYPE: Argentina. Prov. Santa Cruz: San Julián, río Deseado, 1899, *C. Ameghino s.n.* (holotype, LP not seen; isotypes, CONC–28803, F–657367).

Oreopolus glacialis var. *pilosus* Ricardi, Rev. Fac. Ci. Agrar. 13(1–2): 4. 1968. TYPE: Argentina. Prov. San Rafael: Alto Valle del Atuel, Quebrada del Arroyo Nield, 3100 m, 9–17 Jan. 1954, *A. Ruiz Leal 15678* (holotype, herb. H. Ruiz Leal, not seen; isotype, CONC).

Plants forming dense lawns or cushions to 75 cm diam., glabrous or moderately to densely puberulous, usually 3–8 times branched, from tap-roots to 15 mm thick, with red somewhat corky bark; stems 2–10(20) cm long, suberect. *Leaves* with petioles 2–7 mm long; *blades* 8–15 mm long, 2–6 mm wide, at apex acute, at base acute to rounded; *stipules* 1–3 mm long, smooth to somewhat costate, acute to mucronate or bilobed with mucro or lobes to ca. 0.5 mm long. *Inflorescences* ca. 1 cm long and wide excluding corollas; *flowers* with hypanthium 1–2 mm long, pilosulous; *calyx* limb membranaceous, glabrescent, (1)3–4 mm long, divided for ¼–½, lobes (0.5)1–2 mm long and wide, triangular to lanceolate, acute to emarginate or shortly bilobed; *corolla* pale to bright yellow, puberulous to pilosulous externally (abaxially), tube 13–16 mm long, 0.3–0.5 mm diam. near middle, enlarged throat of long-styled form 1.5–2 mm long and in diam., lobes 4–5.5 mm long, 1–1.5 mm wide at base; *anthers* 1–1.5 mm long, filaments 1–1.5 mm long in short-styled form; *stigmas* 0.3–0.5 mm long, in long-styled form exerted by 1–5 mm. *Capsules* 5–8 mm long, 3–6 mm wide, pilosulous; *seeds* 4–6 mm long, 2–3 mm wide. Illustration: Ricardi (1963a: fig. 3).

Distribution and habitat. Southern Andean Cordillera, central Chile and Argentina to Tierra del Fuego (32°–53°S), at 2500–3500 m in the northern part of its range, to as low as 300 m in the southern part, usually in open sand, rubble, or hard soil. Collected in flower October through March, in fruit December through March.

The leaves and stems of *Oreopolus glacialis* range from smooth to markedly papillose, with enlarged epidermal cells, throughout its range. In general, surface texture is correlated with plant size: plants with relatively small leaves and short internodes are usually smooth, while those with relatively large leaves and expanded internodes are papillose. No geographic pattern or correlation

with other characters is evident for plant size, which probably varies primarily with microhabitat.

The unpublished names “*Cruckshanksia oblonga* F. Meigen,” “*Conchospermum oblongum* Phil.,” “*Conchospermum ovatum* Phil.,” “*Conchospermum nudicaulis* Phil.,” “*Oreocaryon nivalis* Kuntze ex K. Schum.,” “*Oreopolus oblonga* Phil. ex F. Meigen,” and “*Oreopolus oblongus* Phil.” have all been used for *Oreopolus glacialis*. Although some of these names have been listed in synonymy with *Oreopolus glacialis* in previous treatments, none of them has been validly published.

Ricardi originally separated variety *pilosus* Ricardi from the typical variety by its “leaves pubescent on both sides, without glandular punctations,” in contrast to the “leaves glabrous with brown glandular punctations abundant on the lower surface” of variety *glacialis* (Ricardi, 1973: 218; my translation from the Spanish text). Occasional plants of *Oreopolus glacialis* from throughout its range are pubescent on vegetative parts with trichomes 0.1–0.2 mm long, and these seem to be the plants that Ricardi intended to segregate as variety *pilosus*. No difference is evident in the density, character, and distribution of pubescence on flowers and fruits of plants he placed in the two varieties. All of the representatives of “var. *pilosus*” were collected near San Carlos de Bariloche in southern Argentina, where vegetatively glabrous plants have been collected apparently sympatrically (e.g., *Buchtien s.n.*, CONC). The structures that Ricardi (1963a) described as “glandular punctations” are found on occasional specimens from throughout the range of this species. These structures may be found on glabrous or pubescent plants, on only the abaxial leaf surface, on both surfaces, or throughout the vegetative parts of the plant. They do not appear to be actual glands, but rather the collapsed walls of enlarged epidermal cells, and are found only on specimens with a markedly papillose epidermis.

However, some plants from near Bariloche, including the type collection of variety *pilosus*, are unusual in having a reduced calyx limb, ca. 1 mm long (e.g., *Boelcke 10049*). This feature was not cited by Ricardi as distinctive, but does seem to be locally frequent in the populations that Ricardi intended to separate in his variety. This variety is not recognized here, though further study may support its separation (N. Bacigalupo, pers. comm.).

Representative specimens examined. ARGENTINA. **Chubut:** Departamento Languiño, 50 km al S de Tecka, *Correa et al. 10390* (BAB). **Mendoza:** San Carlos, Laguna Diamante, *Boelcke et al. 10049* (BAB). **Neuquen:** Departamento Minas, Huingancó, La Rinconada, *Correa et al. 9992* (BAB). **Río Negro:** Parque Nacional Nahuel Huapi,

subida al Granito, *Boelcke & Correa* 5936 (BAB). **Santa Cruz:** Deseado, Picada Río Deseado-Bahía Nodales, *Correa & Nicora* 3443 (BAB). **Tierra del Fuego:** Estancia Sarmiento, foothills to N of Sierra Beauvoir, *Goodall* 4380 (BAB, MO). CHILE. METROPOLITAN REGION. **Prov. Cordillera:** Paso de los Peladeros, Jan. 1933, *Grandjot & Grandjot s.n.* (CONC, GH), Feb. 1937, *Grandjot s.n.* (MO-1160900). VI REGION. **Prov. Colchagua:** Cordillera Inguiririca, *Pirion* 79 (CONC, GH). VII REGION. **Prov. Curicó:** borders of Lake Planchon, *Zöllner* 8455 (MO), 9696 (MO). **Prov. Talca:** entre Paso Pehuneches y Laguna del Maule, *Ricardi et al.* 980 (CONC). VIII REGION. **Prov. Biobío:** faldeos de Volcán Antuco, 5.5 km al S del Refugio de Sky, *Stuessy & Baeza* 11092 (CONC). IX REGION. **Prov. Malleco:** Volcán Loquimay, *Sparre & Constance* 10936 (CONC). XI REGION. **Prov. Aisén:** Río Cisnes, *Ricardi & Matthei* 515 (CONC). XII REGION. **Prov. Magallanes:** Estancia Penitente, Río Penitente, near bridge crossing river to E of St. Palermo, *Moore* 2264 (BAB). **Prov. Ultima Esperanza:** Las Cumbres, Baguales, *Ricardi & Matthei* 378 (CONC).

Cruckshanksia Hook. & Arn., Bot. Misc. 3: 361. 1833, nom. cons., not *Cruckshanksia* Miers, Trav. 2: 529. 1826, Iridaceae, Type = *Cruckshanksia graminea* Miers; not *Cruckshanksia* Hook., Bot. Misc. 2: 211. 1831, Geraniaceae or Ledocarpaceae, Type = *Cruckshanksia cistiflora* Hook. [= *Balbisia peduncularis* (Lindl.) D. Don]. TYPE: *Cruckshanksia hymenodon* Hook. & Arn.

Rotheria Meyen, Reise um die Erde 1: 402. 1834. TYPE: *Rotheria lanceolata* Meyen (= *Cruckshanksia hymenodon* Hook. & Arn.).

Annual or perennial herbs or shrubs, usually geophytic or hemicryptophytic from a woody taproot, glabrescent to usually pubescent, with raphides; stems quadrate to subterete or irregularly channeled, internodes generally expanded; cotyledons usually persistent and photosynthetic on annual plants of *C. pumila*. Leaves opposite or sometimes subopposite to alternate at more distal nodes, simple or sometimes deeply 2–3-lobed, shortly petiolate to sessile; blades elliptic to narrowly so, without domatia; venation subpalmate with 1–2 pairs of strongly ascending secondary veins or sometimes not evident; stipules interpetiolar, free or fused to petioles or leaf bases, on more basal nodes generally triangular to shortly bilobed with margins entire to shortly erose, on more distal nodes more deeply to completely bilobed with margins erose, the erose appendages sometimes elongate (“escamas” sensu Ricardi & Quezada, 1963) or the stipules reduced or absent when leaves lobed. Inflorescences terminal, congested-cymose to subcapitate, branched (0)2–8 times; flowers (1)3–15, distylous, subsessile, each subtended by a foliaceous bract, these simple to

deeply 3–7-lobed, similar to cauline leaves in size, texture, color, and venation, sessile, deeply 3–7-lobed, entire to erose with prolonged linear appendages; hypanthium cylindrical to turbinate or subglobose, densely pilosulous to villous; ovary inferior, bilocular, ovules 2 per locule, anatropous, borne on placentas attached to septum and prolonged into a partial pseudoseptum; calyx limb deeply 2–5(6)-lobed, lobes often erose with linear appendages (“escamas calicinales” sensu Ricardi & Quezada, 1963), equal (*C. macrantha*, *C. palmae*, *C. lithiophila*) or strongly unequal (remaining species), narrowly triangular to elliptic or sometimes prolonged into a stipitate petaloid appendage, this elliptic to ovate, membranaceous, reticulate-veined, puberulent to glabrescent, brightly colored (semaphylls; “uñas,” “sépalos petaloides” sensu Ricardi & Quezada, 1963); corolla slenderly salverform, bright to deep yellow, externally (abaxially) puberulent to pilosulous, internally glabrous, in short-styled form the tube uniform, in long-styled form the tube swollen at top (“garganta” sensu Ricardi & Quezada, 1963), lobes 5, triangular to lanceolate, acute, valvate; stamens 5, in short-styled form inserted at top of corolla tube, exerted, with flattened filaments, in long-styled form inserted at base of enlarged throat of corolla tube, included, subsessile, anthers in both forms basifixed, narrowly ellipsoid-oblong, dehiscent by longitudinal slits; styles filiform; stigmas 2, linear, papillose adaxially, pilose abaxially, in short-styled form borne near middle of corolla tube, in long-styled form exerted by several mm; disk rudimentary. Infructescences sometimes somewhat more expanded and open than inflorescences but otherwise similar; fruits capsular, subglobose to ellipsoid-oblong or ovoid, somewhat didymous, papyraceous to chartaceous, dehiscent loculicidally, acropetally, and often irregularly into 2–5 valves, calyx persistent, often enlarging, with petaloid appendages (pterophylls) becoming ovate or orbicular to reniform, rounded to truncate or emarginate at apex, rounded to usually cordate at base, dry, papery, whitened to yellowed or brown; seeds ellipsoid to ovoid, somewhat compressed, sulcate at attachment, brown to black, smooth to verrucose.

Seven species of arid regions from the Pacific coast to the Andean Cordillera in northern Chile, two species (*Cruckshanksia hymenodon*, *C. macrantha*) extending into adjacent Argentina.

KEY TO SPECIES OF *CRUCKSHANKSIA*

- 1a. Calyx lobes equal, none bearing petaloid appendages or all lobes bearing them, elliptic to oblanceolate or with stipitate elliptic to ovate blades or appendages in flower, these sometimes becoming orbicular to broadly elliptic in fruit.
 - 2a. Leaf blades 15–40 mm long, sharply acute at apex; stipules 1.5–2 mm long; calyx lobes in flower 10–15 mm long, in fruit 12–23 mm long, without stipes 1. *C. palmae*
 - 2b. Leaf blades 8–20 mm long, obtuse to rounded at apex; stipules 0.8–6 mm long; calyx lobes in flower 3.5–11 mm long, including stipe when present, in fruit 7–17 mm long, elliptic to oblanceolate, and without stipes or 9–13 mm long, ovate, and with stipes 10–15 mm long.
 - 3a. Calyx lobes elliptic to oblanceolate, without stipes, in flower 3.5–5 mm long, in fruit 7–17 mm long 2. *C. macrantha*
 - 3b. Calyx lobes in flower composed of stipes 3–6 mm long each bearing an elliptic to ovate appendage 3–5 mm long, in fruit the stipes 10–15 mm long with appendages ovate, 9–13 mm long 3. *C. lithiophila*
- 1b. Calyx lobes unequal, 1–3(4) bearing petaloid appendages, these orbicular to broadly elliptic in flower, and the remaining (0)1–4 lobes elliptic to narrowly triangular or subulate.
 - 4a. Plants annual or rarely apparently perennial; corolla lobes 1–2.5 mm long; corolla tube 0.1–0.3 mm diam. near middle 5. *C. pumila*
 - 4b. Plants perennial; corolla lobes 2–4.5 mm long; corolla tube 0.3–1 mm diam. near middle.
 - 5a. Petaloid calyx appendages pink or white (frequently drying yellow); leaves 2–9.5(15) mm wide 4. *C. hymenodon*
 - 5b. Petaloid calyx appendages yellow; leaves 0.8–4(6) mm wide.
 - 6a. Cauline leaves simple or sometimes 3-lobed; petaloid calyx lobe appendages 6–10 mm long and 8–15 mm wide in flower, to 12 mm long and 18 mm wide in fruit 6. *C. montiana*
 - 6b. Cauline leaves simple to usually 2–3-lobed; petaloid calyx lobe appendages 3–6 mm long and 2–7 mm wide in flower and fruit 7. *C. verticillata*

1. *Cruckshanksia palmae* Clos, in Gay, Fl. Chil. 3: 194. 1848. *Oreopolus palmae* (Clos) Ricardi, Gayana, Bot. 6: 12. 1963. TYPE: Chile. IV Region. Prov. Coquimbo: “cerros arenosos de Guanta [sic; Huanta] en el valle de Coquimbo a una altura de 6 ó 7,000 pies” [1935–2260 m], Nov. 1836, *C. Gay s.n.* (holotype, P not seen; isotype, SGO).

Perennials, densely puberulous to villosulous throughout, from well-developed taproots to 5(10) mm thick, with red bark frequently peeling in plates; stems usually 5–10, to 15 cm long, weak. *Leaves* simple, subsessile; *blades* elliptic to narrowly so, 15–40 mm long, 4–7 mm wide, sharply acute at apex, acute to attenuate at base, subcoriaceous; *stipules* at more basal nodes deltoid to broadly triangular, 1.5–2 mm long, acute to shortly bifid or bilobed, entire to slightly erose, at more distal nodes deeply bilobed, lobes triangular to ligulate, 2.5–4 mm long, acute to acuminate, erose. *Inflorescences* 1–4 cm long and wide excluding corollas; bracts with lobes narrowly elliptic to oblanceolate, acute to acuminate at apex, acute at base, central lobe 24–35 mm long, 3.5–10 mm wide, lateral lobes 2, 14–28 mm long, 2–4 mm wide; *flowers* with hypanthium ca. 1 mm long; *calyx* limb pilosulous, lobes (4)5, equal, elliptic to oblanceolate, 10–15 mm long, 2–5 mm wide, acute at apex and base, entire or erose with minute appendages; *corolla* externally moderately to densely pilosulous, tube 18–

24 mm long, 0.4–0.8 mm diam. near middle, enlarged throat of long-styled form 2–3 mm long and 2.5–3 mm diam., lobes (4)5, 4–5 mm long, 1–2 mm wide at base; *anthers* 2–2.5 mm long, filaments 1.5–2 mm long in short-styled form; *stigmas* 0.5–1 mm long, in long-styled form exerted by 2–3 mm. *Capsules* ca. 5 mm long and wide, persistent calyx lobes 12–23 mm long, 3–5 mm wide; *seeds* 2–3 mm long, 1–2 mm wide. Illustrations: Ricardi (1963a: fig. 4, as “*Oreopolus palma*”), Squeo et al. (1994: fig. 78, as “*Oreopolus palmae*”).

Distribution and habitat. Andean Cordillera of central Chile (30°–33°30’S) at 2000–4000 m, in open sand or rubble. Collected in flower November through March, in fruit January through March.

This species is distinguished by its simple cauline leaves that are acute at the apex, and five calyx lobes that are all similar in form and size, elliptic to oblanceolate, and 10–15 mm long in flower becoming 12–23 mm long in fruit. It is similar vegetatively to *Cruckshanksia hymenodon*, which can be distinguished by its usually two or three petaloid calyx lobe appendages, and to *C. macrantha*, which can be distinguished by its leaves, which are 8–15 mm long and obtuse to rounded at the apex. The consistently trilobed inflorescence bracts were not included in Ricardi’s (1963a) description of this species. The fruits are described for the first time here.

The specific epithet commemorates Señor Ga-

briel Palma, so although it was originally published as "*palma*," it must be corrected to "*palmae*." The name "*Cruckshanksia virescens* Clos" was written on labels of at least one of Gay's collections of this species, but was never published.

Representative specimens examined. CHILE. IV REGION. **Prov. Choapa:** 2 hrs. by horse E of Cuncumen, *Morrison 16999* (CONC, GH). **Prov. Elqui:** at dam, La Laguna, ca. 108 km from Rivadavia, *Johnston 16388* (GH, K, MO). **Prov. Limari:** Río Blanco, *Jiles 1124* (CONC, M). V REGION. **Prov. Cordillera:** in valle San Ramón, *Grandjot s.n.* (CONC-1074, CONC-55546, M, MO-1063540, MO-116091).

2. *Cruckshanksia macrantha* Phil., *Linnaea* 33: 97. 1864. *Oreopolus macranthus* (Phil.) Ricardi, *Gayana, Bot.* 6: 14. 1963. TYPE: Chile. IV Region. Prov. Coquimbo: Quebrada Escondida, 1860–1861, *Volckmann s.n.* (holotype, SGO-56866; isotype, CONC-43455).

Perennials, densely and finely puberulent to villosulous throughout, forming mats to 1 m or more diam., from well-developed taproots to 5(10) mm thick with red bark often peeling in large flakes; stems 3–30, to ca. 15 cm long, weak. *Leaves* simple, subsessile; *blades* narrowly to rather broadly elliptic to lanceolate, oblanceolate, or ligulate, 8–15 mm long, 2–5 mm wide, obtuse to rounded at apex, acute to rounded and then abruptly attenuate at base, subcoriaceous; *stipules* at more basal nodes broadly triangular, 0.8–1 mm long, acute to usually bilobed or shortly bifid, entire to slightly erose, at more distal nodes deeply bilobed, lobes triangular to ligulate, 0.8–1 mm long, acute to rounded, erose. *Inflorescences* 1–2 cm long and wide excluding corollas; bracts with lobes narrowly elliptic to oblanceolate, acute to rounded at apex, acute to attenuate at base, central lobe 4–11 mm long, 1–5 mm wide, lateral lobes 2, 4–10 mm long, 1–2 mm wide; *flowers* with hypanthium 1.5–2[2.5] mm long; *calyx* limb densely pilosulous, lobes (4)5, equal, elliptic to oblanceolate, 3.5–5 mm long, 0.8–2 mm wide, acute at apex and base, entire or erose with appendages 0.5–1 mm long; *corolla* externally moderately to densely pilosulous, tube 18–23 mm long, 0.3–0.6 mm diam. near middle, enlarged throat of long-styled form 2–3 mm long and 1.5–2 mm diam., lobes 5, 4–6 mm long, 1–2 mm wide at base; *anthers* 1.5–2 mm long, filaments 1–1.5 mm long in short-styled form; *stigmas* 0.5–1[2] mm long, in long-styled form exerted by 1–3 mm. *Capsules* 3–5 mm long, 3.5–8 mm wide, persistent calyx lobes 7–17 mm long, 2.5–10 mm wide; *seeds* 2.5–3 mm long, 1.5–2 mm wide. Illustrations: Ricardi (1963a:

fig. 5, as "*Oreopolus macranthus*"); Squeo et al. (1994: fig. 77, as "*Oreopolus macranthus*").

Distribution and habitat. Andean Cordillera of northern Chile and adjacent Argentina (26°30'–32°15'S) at 1100–4300 m, most frequently collected above 3000 m. Collected in flower November through February, in fruit January through February.

This species is distinguished by its simple cauline leaves that are obtuse to rounded at the apex, and by the five calyx lobes that are similar in form and size, elliptic to oblanceolate, and 3.5–5 mm long in flower becoming 7–15 mm long in fruit. It is similar to *Cruckshanksia lithiophila*, which can be distinguished by its calyx lobes all bearing petaloid appendages with slender stipes; these species may not be distinct (see discussion under that species). It is also similar to *C. palmae*, which can be distinguished by its leaves which are 15–40 mm long and acute at the apex. The consistently trilobed inflorescence bracts were illustrated for this species by Ricardi (1963a: fig. 5D) but not included in his description. The fruits are described for the first time here.

Representative specimens examined. ARGENTINA. **San Juan:** Junta del Río Cura, Río de la Tagua below its confluence with the Río de la Sal, *Johnston 6162* (CONC, F, GH). CHILE. III REGION. **Prov. Chañaral:** cerca del Salar de Pedernales, *Zöllner s.n./herb. Garaventa 5324* (CONC), *Zöllner 786* (CONC). **Prov. Copiapó:** Cordillera Río Turbio, Cerro Cadillal, *Werdermann 936* (CONC, E, F, GH, M, MO, NY). **Prov. Huasco:** Laguna Valeriano, *Johnston 6065* (CONC, F, GH, K). IV REGION. **Prov. Choapa:** Río Piuquenes, *San Román s.n.* (CONC-29868). **Prov. Elqui:** Baños del Toro, Doña Ana, *Werdermann 222* (CONC, E, F, GH, K, MO).

3. *Cruckshanksia lithiophila* Ricardi, *Gayana, Bot.* 7: 3. 1963. TYPE: Chile. III Region. Prov. Copiapó: Quebrada Vizcachas, a 43 km de La Puerta, 3100 m, 1 feb. 1963, *M. Ricardi, C. Marticorena & O. Matthei 659* (holotype, CONC-28752; isotype, SGO-73933).

Perennials, puberulent to densely villosulous throughout, from well-developed taproots to 2.5 cm thick with red corky bark; stems 10–30, to ca. 10 cm long, weak. *Leaves* simple, subsessile; *blades* lanceolate to elliptic, 5–20 mm long, 2–7 mm wide, obtuse at apex, attenuate at base, subcoriaceous; *stipules* at more basal nodes triangular, 1–2 mm long, acute to usually bilobed, erose, at more distal nodes deeply bilobed, lobes triangular, 1–6 mm long, acute, erose. *Inflorescences* 1–2.5 cm long and 1–4 cm wide excluding corollas; bracts with lobes narrowly elliptic to oblanceolate, acute to rounded

at apex and base, central lobe 9–21 mm long, 3–6 mm wide, lateral lobes 2, 9–18 mm long, 2–5 mm wide; *flowers* with hypanthium 1–1.5 mm long; *calyx* limb villosulous, lobes 5, equal, entire or erose with appendages 0.5–3 mm long, with stipes 3–6 mm long, appendages elliptic to ovate, 3–5 mm long, 2–4 mm wide, obtuse to rounded at apex, cuneate at base, somewhat petaloid, color unknown; *corolla* externally pilosulous, tube 10–14.5 mm long, 0.3–0.8 mm diam. near middle, enlarged throat of long-styled form 1.5–3 mm long and 1.5–2 mm diam., lobes 5, 2–3 mm long, 1–1.5 mm wide at base [Ricardi (1963b) said 2–2.5 mm long, but his illustration shows the lobes ca. 4 mm long if the proportions are correct]; *anthers* 1–1.5 mm long, filaments 1–1.5 mm long in short-styled form; *stigmas* 1–1.5 mm long, in long-styled form exerted by 1–2 mm. *Capsules* 4–4.5 mm long, ca. 4 mm wide, persistent calyx lobes with stipes 10–15 mm long and appendages ovate, 9–13 mm long, 5–8 mm wide, acuminate; *seeds* 3–4 mm long, ca. 2 mm wide. Illustrations: Ricardi (1963b: figs. 1, 2); Ricardi and Quezada (1963: fig. 2).

Distribution and habitat. Andean Cordillera of northern Chile (27°–27°50'S) at 3300–3600 m, in open rubble. Collected in flower and fruit generally concurrently in November, January, and March.

This infrequently collected species is distinguished by its simple cauline leaves that are obtuse at the apex, and by the five calyx lobes that are each composed of a stipe and petaloid appendage. It is similar and probably closely related to *Cruckshanksia macrantha*, which is distinguished by its elliptic to oblanceolate calyx lobes that are narrowed but not stipitate at the base and generally shorter (3.5–5 mm long in flower and 7–17 mm long in fruit). These two species are maintained here, although considering the variability found in other species of *Cruckshanksia*, *C. lithiophila* may represent only a well-marked variant of *C. macrantha*. The difficulty of distinguishing these species is demonstrated by *Werdermann 936*: the specimens at F and NY were annotated by Ricardi as "*Oreopolus macranthus*" (i.e., *C. macrantha*), while the specimen at GH, which appears similar in all respects, was identified by him as *C. lithiophila*.

The petaloid calyx lobe appendages are usually not well developed at anthesis but enlarge markedly as the fruit develops. Ricardi's description (1963b) does not make this distinction; his measurements apply to the fruiting stage.

Additional specimens examined. CHILE. III REGION. **Prov. Copiapó:** quebrada Chinchas, vega Chinchas, *Marticorena et al. 537* (CONC); quebrada El Colorado, a

mitad de falda, *Marticorena et al. 582* (CONC); quebrada de Vizcachas, *Ricardi & Marticorena 3779* (CONC); camino internacional de Copiapó a Tinogasta, quebrada Coedo, *Villagrán & Arroyo 4668* (CONC).

4. *Cruckshanksia hymenodon* Hook. & Arn., Bot. Misc. 3: 361. 1833. TYPE: Chile. IV Region. Prov. Coquimbo: Coquimbo, *Cruckshanks 3* (lectotype, designated here, E). **SYNTYPES:** Chile. IV Region. Prov. Coquimbo: Coquimbo, *Cuming 861* (K), = *Cruckshanksia montiana*; *Cuming 875* (K), = *Cruckshanksia montiana*.

Rotheria lanceolata Meyen, *Reise um die Erde* 1: 402. 1843. TYPE: Unknown.

Cruckshanksia bustillosii Phil., *Linnaea* 28: 696. 1858. *Cruckshanksia hymenodon* var. *bustillosii* (Phil.) Ricardi, *Gayana, Bot.* 9: 16. 1963. TYPE: Chile. Region Metropolitana: Prov. Santiago: Cordillera de la prov. de Santiago, 1857, *Bustillos s.n.* (holotype, SGO-56889, photo GH).

Perennials, densely villous to pilosulous throughout, from well-developed taproots to 1(2) cm thick with corky reddened bark; stems 3–10, 15–30 cm long, weak. *Leaves* simple or rarely 2–3-lobed, petioles 1–3 mm long; *blades* elliptic to narrowly so or lanceolate, 7–30[40] mm long, 2–9.5[15] mm wide, acute at apex, attenuate at base, membranaceous to subcoriaceous; *stipules* at more basal nodes triangular, 2–4 mm long, acute to bilobed, entire to erose, at more distal nodes deeply bilobed, lobes triangular, 2–4 mm long, acute to acuminate, erose with appendages to 1 mm long. *Inflorescences* 1–3 cm long and 2–10 cm wide excluding corollas; bracts with lobes elliptic to narrowly so, acute at apex and base, central lobe 10–13 mm long, 3–7 mm wide, lateral lobes 2(4), 8–12 mm long, 1–5 mm wide; *flowers* with hypanthium 1–1.5 mm long; *calyx* limb pilosulous to glabrescent, lobes (4)5(6), erose with appendages 0.4–5 mm long, unequal, (1)2–3(4) lobes with stipes 2–9 mm long, appendages ovate to suborbicular or oblong, 3–11 mm long, 2.5–11 mm wide, rounded to truncate at apex and base, petaloid, pink or sometimes white (often drying yellow), remaining lobes subulate and 4–10 mm long or infrequently similar to lobes of bracts and 3–8 mm long by 1–2 mm wide; *corolla* externally moderately to densely pilosulous, tube 9–23[26] mm long, 0.3–1 mm diam. near middle, enlarged throat of long-styled form 1.5–3[4] mm long and 1.5–2 mm diam., lobes 5, 3–4 mm long, 1–2 mm wide at base; *anthers* 1.5–2[2.5] mm long, filaments 1–2 mm long in short-styled form; *stigmas* 1–2 mm long, in long-styled form exerted by 1–3 mm. *Capsules* 3–4 mm long, 3.5–4 mm wide, persistent calyx lobes with stipes 4–9 mm long and appendages 5–11 mm long, 4–

11 mm wide; *seeds* ca. 2 mm long, ca. 1 mm wide. Illustrations: Ricardi and Quezada (1963: fig. 3), Schumann (1891: fig. 8Q, R).

Distribution and habitat. Northern Chile and adjacent Argentina (26°–33°50'W) in arid regions at 20–2950 m. Collected in flower and fruit usually concurrently, at low elevations in October and November, at high elevations December through March.

This is the most commonly collected species of *Cruckshanksia*. It is distinguished by its dense villos to pilosulous pubescence on all vegetative parts, usually simple cauline leaves, and calyx with usually 2–3 lobes bearing pink or white petaloid appendages. Label data often describe the color of either the petaloid calyx appendages (pink or white) or the corollas (yellow) without specifying which structure is described, and this has been the source of some confusion. Additionally, the pink petaloid appendages frequently become yellow when dried.

In the original description of *Cruckshanksia hymenodon*, Hooker and Arnott noted that two different forms could be distinguished, “ α . foliis incanis” and “ β . foliis minus pubescentibus,” and cited a collection made by Cruckshanks for the first and two collections by Cuming for the second. These two forms correspond to what are here considered two distinct species, *C. hymenodon* and *C. montiana*, respectively. Although all previous authors have interpreted these taxa in this way, no one previously has clearly selected a lectotype. This is done here. Even though both of Cuming’s collections have several duplicates and are more widely distributed than the single Cruckshanks specimen, this last specimen is chosen here in order to fix the application of this name to the species to which it was applied by Clos (1848) and all subsequent authors.

Ricardi and Quezada (1963) recognized two varieties in this species: var. *hymenodon* and var. *bustillosii*. They distinguished variety *bustillosii* in their key based on its “linear-lanceolate leaves, sepals 2, corollas 16–20 mm long, and plants with a tendency to form lawns,” in contrast to “leaves mostly oblong-lanceolate, sepals 2–3(5), and corollas 26–30 mm long” in variety *hymenodon* (Ricardi & Quezada, 1963; my translation from the Spanish; no habit information given by them for var. *hymenodon*). They distinguished variety *bustillosii* in their diagnosis and discussion only by its “chamaephytic habit, linear-lanceolate leaves, and emarginate apex of the sepals” (Ricardi & Quezada, 1963; my translation from the Spanish; in their usage, “sepal” denotes only calyx lobes that bear petaloid ap-

pendages). However, many specimens bear some characteristics of both varieties and cannot be classified according to these criteria, including specimens studied by Ricardi and Quezada. For example, *Werdermann 158*, placed by them in variety *hymenodon*, has corollas 18 mm long and petaloid calyx lobe appendages that vary from obtusely angled to truncate or in a few flowers shortly emarginate, and *Wagenknecht 18505* (CONC, GH, MO), also placed by them in variety *hymenodon*, has several petaloid calyx lobe appendages that are as deeply emarginate as those shown in their illustration of variety *bustillosii*, along with others that are obtusely angled. Several leaves on specimens identified as variety *bustillosii* (e.g., *Worth & Morrison 16568*; *Morrison 16998*) are similar in shape to those of typical variety *hymenodon*, although they are generally shorter than the average (but not the extreme) for variety *hymenodon* and some other leaves on the same plant are relatively narrower. The plants segregated as variety *bustillosii* are all from relatively higher elevations, but specimens of variety *hymenodon* are cited from throughout this same range, so no geographic or ecological difference is evident. The plants classified as variety *bustillosii* are generally markedly smaller in stature, and on collections with abundance indicated they are usually said to be rare or infrequent, in contrast to the usual description of the larger, more robust plants of variety *hymenodon* as common or abundant. It seems likely that these plants are no more than reduced representatives of this species, probably due to microhabitat conditions, and this variety is not recognized here.

Representative specimens examined. ARGENTINA. **San Juan:** Departamento Calingasta, al S de Barreal, Mantiales, *Kiesling et al. 8051* (MO, SI). CHILE. III REGION. **Prov. Chañaral:** 19 km al interior de Llanta, *Ricardi et al. 1563* (CONC). **Prov. Copiapó:** ca. 40 km S of Copiapó along Rte. 5, ca. 2 km N of the entrance to Mina Flor del Llano, *Taylor et al. 10781* (CONC, MO), *10782* (CONC, MO). **Prov. Huasco:** Alto del Carmen, *Werdermann 158* (E, GH, K, M, MO). IV REGION. **Prov. Choapa:** La Vega Escondida, 3 hr. by horse E of Cuncumen, *Morrison 16998* (GH, MO). **Prov. Elqui:** Baños del Toro, *Werdermann 211* (E, F, GH, K, M, MO), *Zöllner 10392* (MO). **Prov. Limari:** Los Molles, *Jiles 4762* (CONC, M). V REGION. **Prov. Petorca:** Cerro Chache, 5 hr. by horse SE of Patagua Mine, 18 km E of La Ligua, *Morrison 17025* (GH, MO). REGION METROPOLITANA. **Prov. Cordillera:** Lagunillas, *Zöllner 10644* (MO).

5. *Cruckshanksia pumila* Clos, in Gay, Fl. Chil. 3: 196. 1848. TYPE: Chile. IV Region. Prov. Coquimbo: “vecindad de Arqueros, 8bri 1836,” *C. Gay 242* [holotype, P not seen, photo (neg. #4646) SGO; isotypes, P not seen, photo (neg. #4647) SGO, probable isotype F-972004].

Cruckshanksia tripartita Phil., Viage Des. Atacama 200. 1860. TYPE: Chile. III Region. Prov. Chañaral: Pan de Azucar, R. A. Philippi s.n. (holotype, SGO-56883; isotype, SGO-43336/herb. F. Philippi 951).

Cruckshanksia chrysantha Phil., Anales Univ. Chile 41: 730. 1872. TYPE: Chile. III Region. Prov. Huasco: Yervas Buenas, Oct. 1871, T. King s.n. (holotype, SGO-56904; isotypes, E, GH, K-ex herb. E. C. Reed, photo (neg. #2472) SGO, SGO-43356/herb. F. Phil. 948b, SGO-43348/herb. F. Phil. 948a, photo GH).

Cruckshanksia geisseana Phil., Anales Univ. Chile 85: 737. 1894. TYPE: Chile. III Region. Prov. Copiapó: Cerro Bandurrias, 1885, W. Geisse s.n. (lectotype, designated here, SGO-43365/herb. F. Phil. 1935, photo SGO; isotype, GH).

Cruckshanksia darapskyana Phil., Anales Univ. Chile 85: 738. 1894. TYPE: Chile. II Region. Prov. Antofagasta: Taltal, 1889, Dr. L. Darapsky s.n. (holotype, SGO-56884; isotype, SGO-43346/herb. F. Phil. 2318, photo GH).

Annuals or rarely apparently perennials, puberulent to densely villosulous or pilosulous throughout (above hypocotyl), from a solitary short to well-developed taproot 1–2.5 mm thick with smooth gray or brown epidermis; stems to ca. 15 cm long, usually 1–4 times branched but occasionally more or not at all, ascending to weak; *cotyledons* sessile, narrowly oblanceolate to ligulate, 8–16 mm long, 1.5–3 mm wide, at apex truncate to rounded, at base attenuate, fleshy drying coriaceous, glabrous, with stipules interpetiolar, fused to bases of cotyledons, membranaceous, interpetiolar portion truncate to broadly triangular, 1–2 mm long, entire to shortly bifid or erose. *Leaves* simple or rarely 2-lobed, petioles (0.5)2–7 mm long; *blades* elliptic to usually narrowly so or oblanceolate, (4)12–30 [40] mm long, (2)3–8 mm wide, acute at apex, acute to usually attenuate at base, membranaceous to subcoriaceous; *stipules* at more basal nodes deeply bilobed, lobes triangular to narrowly so, 1–4 mm long, acute to acuminate, erose with appendages to ca. 1 mm long, at more distal nodes similar or more deeply lobed to completely divided. *Inflorescences* 1–2.5 cm long and 1–6 cm wide excluding corollas; bracts with lobes elliptic to narrowly so, acute at apex and base, central lobe 8–34 mm long, 3–4 mm wide, lateral lobes 2(4), 5–15 mm long, 2–4 mm wide; *flowers* with hypanthium 0.5–1.5 mm long; *calyx* limb pilosulous, lobes 4–5, erose with appendages 1–4 mm long, unequal, (0)1–2 lobes with stipes 2–7 mm long, appendages elliptic to suborbicular, 2–10 mm long, 5–10 mm wide, obtusely angled to rounded or subtruncate and usually mucronate at apex with mucro 0.5–1 mm long, rounded to truncate or somewhat cordate at base, petaloid, bright to deep yellow, remaining lobes subulate, 2.5–8 mm long; *corolla* externally moder-

ately to densely pilosulous, tube 9–12 mm long, 0.1–0.3 mm diam. near middle, enlarged throat of long-styled form 1–1.5 mm long and diam., lobes 5, 1–2.5 mm long, 0.5–1 mm wide near base; *anthers* 1–1.3 mm long, filaments 1–1.5 mm long in short-styled form; *stigmas* 1–2 mm long, in long-styled form exerted by 1–1.5 mm. *Capsules* 2–3 mm long, 2–3.5 mm wide, persistent calyx lobe appendages to 13 mm long, 15 mm wide; *seeds* ca. 1.5 mm long, ca. 1 mm wide. Illustrations: Ricardi and Quezada (1963: Fig. 5, as “*C. tripartita*,” and Fig. 9 but in Fig. 9A the stipules at more distal nodes are not entirely accurate and Fig. 9B shows a stipule of a relatively basal node).

Distribution and habitat. Northern Chile (23° 30′–30°10′S) at 10–1900 m, in arid regions. Collected in flower and fruit concurrently, September through December.

This frequently collected species is distinguished by its annual habit, usually simple cauline leaves, calyx with usually 1–2 lobes prolonged into yellow petaloid appendages, and relatively small flowers with slender tubes.

Ricardi and Quezada (1963) separated *Cruckshanksia tripartita* from *C. pumila*, commenting that Johnston (1929) had combined them but the taxa seemed distinct. Philippi in his original description separated *C. tripartita* based on its larger, more branched inflorescence, but this feature intergrades continuously with plants he placed in *C. pumila* and appears to represent only an advanced developmental stage. Ricardi and Quezada commented in their discussion under *C. tripartita* that these species are separated by their “habit, pubescence, stipules, and floral characteristics” (my translation from the Spanish), but in their key to species they separated these only by the stipules “non-interpetiolar, setaceous, entire, to 4 mm long” in *C. tripartita* in contrast to “interpetiolar, triangular-long acuminate, lacinate-ciliate, to 2 mm long” in *C. pumila*. As discussed in the morphology section (above), these stipule forms represent developmental stages that may be found on the same stem, and both conditions are found on most specimens cited for each of these species by Ricardi and Quezada. This stipule distinction thus serves primarily to separate plants that flower precociously from those that show more vegetative development. When the distinctions in this key are applied, the individual plants of one population are sorted into two species (e.g., Taylor 10764, CONC, MO; 10793, CONC, MO). No pattern is evident in any other features, and *C. tripartita* is here combined with *C. pumila*.

Ricardi and Quezada (1963) cited “Huanta, in

collibus arenosis, 8bri 1836', leg. *C. Gay* (SGO)," as the "isotype" of *Cruckshanksia pumila*. These data correspond to two specimens, CONC-28802 and SGO-56885, which additionally both bear the collection number 1929. However, this information does not agree with the locality cited in the original species description, "en los arenales porfíricos de la vecindad de Arqueros," so these specimens apparently are not types. Ricardi and Quezada (1963) listed several Geisse collections made in 1885 and 1886 and deposited at SGO as "types" and one at GH as an "isotype" of *C. geisseana*. Philippi gave the type locality for this species as "prope Banderrias haud procul a Chañarcillo detexit orn. Guilielmus Geisse," and judging from annotations at SGO most likely based his description on most or all of the set of specimens sent to him by William Geisse with collection dates of 1886 or earlier. These specimens are here considered syntypes. From them, the one best represented in several herbaria is chosen here as the lectotype. These collections have been variously attributed to "W. Geisse," "Guill. Geisse," "Guillermo Geisse," and "G. Geisse."

Many of the "perennial" specimens cited by Ricardi and Quezada (1963) represent annual plants with well-developed taproots, or have here been referred to *Cruckshanksia hymenodon*. The few apparently truly perennial specimens of *C. pumila* (*Jaffuel* 2628, CONC, GH; *Jiles* 5370, CONC; *Ricardi & Parra* 77, CONC) are additionally characterized by relatively small leaves and petaloid calyx appendages, although these all fall within the range of sizes found among the annual plants. These plants are all from the Taltal area, and may represent a distinct population. Only the apparently perennial habit distinguishes them, however, and they are here provisionally included in *C. pumila*.

Representative specimens examined. CHILE. II REGION. **Prov. Antofagasta:** Taltal, near Paposo, Cerro Yumbes, *Johnston* 5560 (CONC). III REGION. **Prov. Chañaral:** Carretera Panamericana, entre Las Bombas y Chañaral, Km 27, *Ricardi et al* 1430 (CONC). **Prov. Huasco:** Rte. 5 between Domeyko and Vallenar, ca. 20 km N of Domeyko, *Taylor et al.* 10679 (CONC, MO). **Prov. Copiapó:** entre Vallenar y Copiapó, a 39 km de Copiapó, *Ricardi et al.* 663 (CONC). IV REGION. **Prov. Elqui:** Rivadavia, *Montero* 11687 (CONC), *Ricardi* 2178 (CONC). **Prov. Limari:** Corral Quemado, *Jiles* 3484 (CONC).

6. *Cruckshanksia montiana* Clos, in *Gay*, Fl. Chil. 3: 195. 1848. TYPE: Chile. IV Region. Prov. Coquimbo: "dunas cerca de La Serena, 7bri 1836," *C. Gay* 1931 (holotype, P not seen; isotypes, CONC-43456, GH, K, NY, SGO-56880, and possibly F-635148).

Cruckshanksia capitata Philippi, Anal. Univ. Chile 41: 731. 1872. TYPE: Chile. III Region. Prov. Huasco: Carrizal Bajo, *T. King* s.n. (holotype, SGO-56879; isotype, SGO-43367/herb. F. Phil. 944, photo GH). *Cruckshanksia densifolia* Philippi, Anal. Univ. Chile 41: 730. 1872. *Cruckshanksia capitata* var. *densifolia* (Philippi) Reiche, Anal. Univ. Chile 106: 973. 1900. TYPE: Chile. III Region. Prov. Huasco: Carrizal Bajo, 1871, *T. King* s.n. (holotype, SGO-56882, photo GH; isotype, E).

Perennials, puberulent to densely villosulous throughout, from well-developed taproots 1.5 cm thick with red corky bark; stems 5–15, to ca. 20 cm long, weak. *Leaves* simple with petioles 1–5 mm long or sometimes 3-lobed and sessile; *blades* narrowly elliptic, 8–23 mm long, 0.8–4(6) mm wide, acute and sometimes mucronate at apex with mucro to ca. 0.5 mm long, attenuate at base, membranaceous to subcoriaceous; *stipules* at more basal nodes triangular, 1–3 mm long, acute to shortly bilobed, entire to slightly erose, at more distal nodes deeply bilobed, lobes triangular to narrowly so, 1.5–7 mm long, acute, erose with appendages to ca. 1 mm long. *Inflorescences* 1–3.5 cm long and 2–4.5 cm wide excluding corollas; bracts with lobes narrowly elliptic to narrowly oblanceolate, acute at base and apex, central lobe 10–17 mm long, 1.5–4 mm wide, lateral lobes 2–4, 8–15 mm long, 1–2.5 mm wide; *flowers* with hypanthium 1.5–2 mm long; *calyx* limb pilosulous, lobes (4)5(6), erose with linear appendages 0.5–4 mm long, unequal, (1)2–3(4) lobes with stipes 6–10 mm long, appendages orbicular to oblong or somewhat reniform, 6–10 mm long, 8–15 mm wide, rounded to usually truncate and mucronate at apex with mucro 0.5–1 mm long, rounded to truncate at base, petaloid, bright to deep yellow, remaining lobes subulate and 4–10 mm long or occasionally similar to bracts, 3–8 mm long, 0.5–1.5 mm wide; *corolla* externally moderately to densely pilosulous, tube 10–13 mm long, 0.3–0.6 mm diam. near middle, enlarged throat of long-styled form 1–1.5[3] mm long and diam., lobes 5, 2–4.5 mm long, 1–2 mm wide at base; *anthers* 1–1.5[2] mm long, filaments ca. 1–2 mm long in short-styled form; *stigmas* ca. 1 mm long, in long-styled form exerted by 1–2 mm. *Capsules* 2.5–3[4] mm long, ca. 3[4] mm wide, persistent calyx lobe appendages to 12 mm long, 18 mm wide; *seeds* 1.5–2 mm long, ca. 1 mm wide. Illustrations: Ricardi and Quezada (1963: fig. 6, fig. 7, as "*C. capitata*").

Distribution and habitat. Northern Chile, in arid regions at 10–500 m. Collected in flower and fruit usually concurrently, September through November.

This species is distinguished by its usually simple narrow cauline leaves with the secondary ve-

nation not evident and calyx with usually 2–3 lobes prolonged into yellow petaloid appendages. It is similar to *Cruckshanksia verticillata*, as discussed under that species.

Ricardi and Quezada (1963) separated *Cruckshanksia capitata* based on the form of the stipules and petaloid calyx lobe appendages. However, as discussed in the morphology section (above), both of these features vary with developmental stage, usually along a single stem. The stipule form by which they distinguished "*C. capitata*" is that characteristic of more basal nodes and the form of the petaloid calyx lobe appendages they used is that found on the flowers, while the forms by which they distinguished "*C. montiana*" are those of the most distal nodes and the fruiting stage, respectively. Most of the specimens they cite show both of the conditions they used to separate these species, and consequently *C. capitata* is here combined with *C. montiana*.

Cruckshanksia montiana was named in honor of Señor Manuel Montt, but originally published with the spelling "*montiana*." This epithet has been improperly corrected by various authors to "*montiana*," and has also been misspelled as "*montteana*" and "*montana*." As discussed in detail under the treatment of *Cruckshanksia hymenodon*, Hooker and Arnott originally based their description of that species on three specimens, two of which represent *C. montiana*.

Representative specimens examined. CHILE. III REGION. **Prov. Copiapó:** Quebrada del León, *Billiet & Jadin 5356* (BR, MO), *Werdermann 434* (CONC, E, GH, K, M, MO). **Prov. Huasco:** Huasco, *Werdermann 133* (CONC, E, GH, K, MO). IV REGION. **Prov. Elqui:** road from La Serena to Punta Teatinos, *West 3918* (CONC, GH, MO).

7. *Cruckshanksia verticillata* Phil., *Anal. Univ. Chile* 85: 737. 1894. TYPE: Chile. II Region. **Prov. Antofagasta:** Bandurrias, 1886, *W. Geisse s.n.* (holotype, SGO-56873/herb. F. Phil. 1936; isotype, SGO-56878, photo GH).

Cruckshanksia paradoxa Phil., *Anal. Univ. Chile* 85: 738. 1894. *Cruckshanksia capitata* var. *paradoxa* (Phil.) Reiche, *Anal. Univ. Chile* 106: 973. 1900. TYPE: Chile. II Region. **Prov. Antofagasta:** Pajonales, Nov. 1887, *W. Geisse s.n.* (lectotype, designated here, SGO-72374).

Perennials, puberulent to villosulous or pilosulous throughout, from well-developed taproots to 6 mm thick with somewhat corky reddened bark; stems 2–10, to 10 cm long, weak. *Leaves* simple to usually 2–3-lobed, subsessile to sessile; *blades* narrowly to very narrowly oblanceolate, 7–18 mm

long, 1–2 mm wide, acute and frequently falcate at apex, attenuate at base, membranaceous to subcoriaceous; *stipules* usually none or with 1 or 2 lobes, these separate, triangular, 1–1.5 mm long, 0.8–1 mm wide, acute to rounded, erose with appendages to ca. 1 mm long. *Inflorescences* 1–2 cm long and 1–3 cm wide including corollas; bracts similar to cauline leaves of most distal nodes; *flowers* with hypanthium 0.5–1 mm long; *calyx* limb villous to pilosulous, lobes 2, erose with linear appendages 0.5–3 mm long, equal, with stipes 4–6 mm long, appendages elliptic-oblong to suborbicular, 3–6 mm long, 2–7 mm wide, rounded and frequently mucronate at apex with mucro ca. 0.5 mm long, acute to cuneate at base, petaloid, yellow; *corolla* externally moderately to densely pilosulous, tube 12–14 mm long, 0.3–0.5 mm diam. near middle, enlarged throat of long-styled form 2–3 mm long and 1.5–2 mm diam., lobes 5, 3–3.5 mm long, 1–1.5 mm wide near base; *anthers* 1–1.3[2] mm long, filaments ca. 1 mm long in short-styled form; *stigmas* ca. 0.5 mm long, in long-styled form exerted by 1–2 mm. *Capsules* ca. 3 mm long and wide, persistent calyx lobe appendages enlarging slightly at most; *seeds* ca. 1.5 mm long, ca. 1 mm wide. Illustration: Ricardi and Quezada (1963: fig. 8).

Distribution and habitat. Northern Chile, in open sand and rubble of arid regions near Taltal at 100–1000 m. Collected in flower and fruit October through November.

This infrequently collected species is distinguished by its cauline leaves with usually two or three narrow lobes, and by the calyx limb reduced to two lobes, both with petaloid appendages. The cauline leaves are generally indistinguishable from the inflorescence bracts. It is similar and probably closely related to *Cruckshanksia montiana*, which can be distinguished by its usually simple cauline leaves and petaloid calyx lobe appendages 7–15 mm wide. Most features of *C. verticillata* are consistently smaller than those of *C. montiana* except the corollas, which are usually slightly longer, although these measurements overlap. These two species are maintained here, although considering the variability found in other species of *Cruckshanksia*, *C. verticillata* may represent only a well-marked variant of *C. montiana*.

The designation of type specimens for *Cruckshanksia verticillata* here follows annotations by Ricardi (in herb.) and citations in Ricardi and Quezada (1963). The lectotype chosen here for *C. paradoxa* is the only one of the syntypes that does not have some confusion attached to the label data.

Additional specimens examined. CHILE. III REGION. **Prov. Copiapó:** Bandurrias, 1885, *W. Geisse s.n.* [SGO-43368/herb. F. Phil. 1918, photo GH], 1885–1886, *W. Geisse s.n.* (GH, SGO-56875); Atacama, *com. Phil. 2/1888* [K not seen photo (neg. #SGO-2478) SGO]. IV REGION. **Prov. Elqui:** Pajonales, Nov. 1886, *W. Geisse s.n.* (SGO-72661).

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- Cabrera 12624 (7). Castellanos 7908 (1). Cei 24176 (1). Comber 263 (1), 841 (1). Cordini 210 (1). Correa 2645 (1), 3059 (1), 3443 (1), 3566 (1), 3796 (1), 6346 (1), 8943 (1), 9091 (1), 9241 (1), 9992 (1), 10056 (1), 10237 (1), 10390 (1), 10442 (1). Covetto 7140 (1). Crespo 1645 (1), 2104 (1), 2287 (1). Cuming 861 (5), 875 (5), 1301 (7), 1302 (2).
- Dawson 2624 (1). Diem 3224 (1). Donat 77 (1), 172 (1), 177 (1), 364 (1).
- Elliot 22 (7). Eskuche 1121 (1).
- Flores 25 (7). Furlong 40 (1).
- Garaventa 4231 (7), 4400 (7), 4732 (2). Gardner 4535 (1). Gay 133 (5), 412 (2), 413 (6), 865 (5), 1255 (1). Gerling 5756 (1). Gigoux 217 (7), 220 (8), 627 (2). Gliesner 29 (7). Goodall 14 (1), 3955 (1), 4283 (1), 4380 (1). Grau 2043 (7), 2109 (7), 2118 (7), 2522 (2), 2540 (7), 2897 (1). Greninger 14 (2).
- Hoffman 43 (7). Hosseus 245 (1), 601 (1), 1324 (1), 1332 (1). Hunziker 4845 (4), 7086 (1).
- Illin 43 (1), 55 (1), 138 (1), 456 (1), 5524 (1), 5526 (1), 5736 (1), 5762 (1), 18146 (1).
- Jaffuel 1158 (7), 2628 (7). Jiles 1124 (6), 1167 (2), 1199 (6), 1301 (7), 1571 (2), 2194 (7), 2225 (7), 2417 (2), 2427 (7), 2486 (6), 2571 (2), 2965 (6), 3147 (7), 3309 (2), 3484 (7), 3687 (7), 3758 (6), 3803 (2), 3917 (2), 3942 (7), 3992 (7), 4079 (2), 4167 (6), 4273 (2), 4762 (2), 4983 (5), 5064 (4), 5107A (2), 5273 (2), 5370 (7), 5442 (7), 5508 (2), 5803 (7), 5812 (2), 6354E (5), 6396 (2), 6505 (4). Johnston 3671 (2), 4784 (7), 4818 (2), 4872 (2), 4910 (2), 4974 (2), 5106 (7), 5160 (7), 5301 (7), 5560 (7), 5595 (7), 5711 (7), 5930 (4), 6065 (4), 6162 (4).
- Kausel 3747 (7). Kiesling 8051 (2). King 26 (7), 51 (2). Krapov 4128 (1), 4288 (1). Krapovickas 5698 (4), 5726 (2). Kurtz 9570 (2). Koslowsky 115 (1), 5528 (1).
- Landero 630 (1). Lechler 2895* (1). Leuenberger 3403 (1). Lobb 435 (5), 436 (7).
- Magens 62 (1). Marticorena 1 (2), 63 (1), 207 (2), 244 (7), 248 (7), 328 (7), 495 (2), 537 (3), 582(3), 1030 (1), 1264 (7), 1387 (1), 1656 (7), 1678 (2), 1684 (2), 1699 (7), 9810 (2). Merxmüller 24996 (1). Meyer 9637 (1). Molina M. 34 (1). Montero 11687 (7). Moore 2264 (1). Morong 54 (2), 55 (7), 107 (8), 1106 (2), 1109 (2), 1303 (5). Morrison 16963 (2), 16998 (2), 16999 (6), 17025 (2), 17443 (2). Muniez 159 (1). Muñoz 2726 (2), 2837 (7), 2955 (7).
- O'Donell 3748 (1).
- Pereyra 2166 (1), 5306 (1). Pérez 23404 (2). Peterson 270.33 (1). Pirion 79 (1), 126 (1). Pisano 3660 (1), 4174 (1), 4730 (1), 4781 (1), 5604 (1). Poeppig 59* (1).
- Rechinger 63338 (7), 63339 (2), 63476 (7), 63494 (7). Ricardi 12 (2), 77 (7), 378 (1), 484 (1), 515 (1), 533 (2), 552 (2), 663 (7), 980 (1), 1102 (2), 1131 (2), 1136 (5), 1250 (7), 1430 (7), 1462 (2), 1489 (2), 1563 (2), 1569 (2), 1718 (2), 1740 (6), 1750 (6), 1783 (4), 1788 (4), 2178 (7), 2232 (2), 2275 (7), 2351 (1), 2459 (7), 2524 (7), 2528 (2), 2586 (7), 2627 (7), 2634 (7), 3051 (7), 3139 (7), 3766 (2), 3779 (3), 3970 (5), 4359 (7), 5074 (1), 5139 (1), 5527 (7), 5663 (1). Rodraguez 10 (2), 77 (5). Rodriguez 40 (2), 1616 (7). Roig 11973 (2), 13019 (2), 13032 (2), 13043 (2). Romanczuk 954 (1). Rosas 1012 (7), 1169 (2), 1248 (2), 1256 (5), 1844 (1). Rose 19338 (7). Rossow 1310 (1), 1325 (1), 1463 (1), 1872 (1), 1617 (1), 1651 (1), 2662 (1), 4565 (1). Ruiz I. 3131 (1), 7175 (1), 11689 (1), 11727 (1), 15678 (1), 15736 (1), 16833 (1), 21441 (1).
- Sánchez 293 (1), 442 (1), 552 (1). Santesson 1272 (1).

Appendix I. Index to numbered collections examined.

Identifications are indicated by numbers in parentheses following the collection number, as below. Asterisks indicate a type collection.

- 1 = *Oreopolus glacialis* (Poepp.) Ricardi
 2 = *Cruckshanksia hymenodon* Hook. & Arn.
 3 = *C. lithiophila* Ricardi
 4 = *C. macrantha* Phil.
 5 = *C. montiana* Clos
 6 = *C. palmae* Clos
 7 = *C. pumila* Clos
 8 = *C. verticillata* Phil.

Arroyo, M. K. 81002 (4), 81042 (4), 81096 (4), 81112B (6), 81227 (2), 81619 (4), 81634 (4), 81681 (2), 83370 (2), 83403 (2), 83464 (4), 84555 (4), 83624 (2), 841003 (1), 850831 (1). Arroyo, S. C. 150 (1), 225 (1), 321 (1), 2243 (1), 2376 (1), 2513 (1), 3339 (1).

Bayern 352 (7). Betfreund 12438 (1). Billiet 5356 (5), 5570 (2). Boelcke 1694 (1), 3382 (1), 3410 (1), 3411 (1), 3546 (1), 5936 (1), 7228 (1), 10049 (1), 11114 (1), 11300 (1), 11669 (1), 13797 (1), 15106 (1), 15837 (1). Bridges

Schlegel 937 (6), 2415 (6), 5716 (5), 5886 (2). Seibert 300 (1). Semper 13992 (2). Senn 4269 (1). Silvestri 5744 (1). Solbrig 3040 (5), 3067 (7). Soriano 2026 (1), 2459 (1), 3067 (1). Sparre 10936 (1). Spegazzini 52 (1), 158 (1), 207 (1), 339 (1). Squeo 88008 (4), 88055 (4), 88082 (4), 88097 (4). Stuchart 18146 (1). Stuessy 11092 (1).

Taylor 10679 (7), 10764 (7), 10781 (2), 10782 (2), 10793 (7). TBPA 455 (1), 539 (1), 740 (1), 1669 (1), 2174 (1), 2330 (1), 2717 (1), 2854 (1), 3619 (1), 3758 (1). Teil-
lier 557 (7), 657 (7), 731 (7), 968-969 [sic] (2).

Vervoorst 5626 (1). Villagrán 4668 (3). Volckmann 64 (2).

Wagenknecht 18120 (2), 18484 (7), 18505 (2), 18553 (7). Werdermann 112 (7), 133 (5), 158 (2), 211 (2), 222 (4), 434 (5), 810 (7), 936 (4). West 3918 (5), 4778 (1). Witte 35 (1). Worth 15835 (7), 16196 (2), 16233 (5), 16270 (2), 16388 (6), 16398 (2), 16565 (6), 16568 (2), 16682 (2).

Zöllner 787 (2), 786 (4), 5324 (4), 6015 (7), 6168 (7), 6196 (7), 6503 (7), 8455 (1), 8720 (7), 9312 (7), 9696 (1), 10002 (2), 10392 (2), 10644 (2), 10928 (5), 11376 (7), 14049 (2), 14819 (2), 18646 (7), 18693 (7), 18906 (2), 19124 (7), 19136 (7), 19138 (2).